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Journal of Arid Environments 59 (2004) 657–674

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Journal of
Arid
Environments

Biomass equations for shrub species of Tamaulipan thornscrub of North-eastern Mexico[☆]

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Received 18 February 2003; received in revised form 30 January 2004; accepted 10 February 2004

Abstract

Nine additive allometric equations for computing above-ground, standing biomass were developed for the plant community and for each of 18 single species typical of the Tamaulipan thornscrub of north-eastern Mexico. Equations developed using additive procedures in seemingly unrelated linear regression provided statistical efficiency in total biomass estimates at the scales of both individual species and at the plant community. A single equation for each species improves efficiency in biomass estimates by 12.5% in contrast to using a single equation for the plant community. Therefore, additive equations developed in seemingly unrelated linear regression of parameter estimation are recommended to compute biomass components and total biomass for the species described.

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Keywords: Above-ground biomass components; Additive least-squares techniques; Arid; Semi-arid and subtropical shrub species

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1. Introduction

Considerable research has gone into estimating the biomass of individual shrub species (Murray and Jacobson, 1982; Frandsen, 1983; N  var et al., 2002). Land managers and researchers require reliable estimates of total tree or component weights to assess site productivity, food abundance, treatment effects, and fuel loading (Kie and White, 1985). Present-day biomass estimates are required to estimate stocks and fluxes of carbon dioxide, CO₂, within the Earth–atmosphere system (Houghton, 1991; Marland et al., 1997; Schimel et al., 2000). Indeed, several CO₂ models require the estimation of biomass or biomass-related parameters to assess the fate of CO₂ in the biosphere (M  kel  , 1997; Marland et al., 1997; Bhatti et al., 1998; Schimel et al., 2000). Given this importance, biomass equations had been compiled or developed for tropical, temperate, and boreal trees or forests (Brown et al., 1989; Schroeder et al., 1997; Ter-Mikaelian and Korzukhin, 1997; Jenkins et al., 2001). However, biomass equations for other ecosystems have been little studied.

To readily estimate biomass components non-destructive techniques are needed, which are rapid, relatively accurate, and have few training requirements. Procedures for biomass estimation of individual trees consist of relating biomass components or total to tree characteristics such as basal diameter or diameter at breast height (Brown, 1997; N  var et al., 2003), crown cover (Harniss and Murray, 1976; Frandsen, 1983), and crown volume (Murray and Jacobson, 1982). Biomass estimations at the stand scale consist of the summation of individual tree biomass components.

The choice of model and the method of fitting parameters are two of the most common features that must be considered when estimating biomass (Woods et al., 1991). A variety of regression models have been developed for estimating total tree biomass or tree-component biomass (Clutter et al., 1983), and they fall into three main forms: (a) linear additive error, (b) nonlinear additive error, and (c) nonlinear multiplicative error (Parresol, 1999). The variety of regression equations for estimating total-tree and tree-component biomass can be classified into non-additive and additive. Non-additive equations compute total biomass neglecting the biomass components, which are usually measured separately. In additive equations the predictions for the components sum to the prediction from the total tree regression (Cunia and Briggs, 1984, 1985; Reed and Green, 1985; Parresol, 1999). Additive methods can be classified in three different procedures depending on how the individual components are aggregated (Cunia and Briggs, 1984; Reed and Green, 1985; Parresol, 1999). The computation of total biomass is ensured by (1) using the same independent variables for estimating each component, (2) adding the best regression functions of each biomass component, and (3) forcing the regression coefficients of the individual biomass components to estimate total biomass (Cunia and Briggs, 1985; Parresol, 1999). The sum of the regression estimates of the biomass components in (1) and (2) frequently does not equal the regression estimates of total biomass. Seemingly unrelated regression is a procedure that forces the coefficients of the component equations to equal the total biomass equation (Cunia and Briggs,

1985; Parresol, 1999). Additive procedures have been used for temperate trees but not for estimating total biomass for shrubs or trees of other ecosystems such as semi-arid, subtropical systems. Indeed, Cunia and Briggs (1985) stressed the importance of testing the applicability of additive techniques in shrubs or trees of other ecosystems.

The aim of this study was (1) to compute equation parameters for estimating biomass components of total above-ground, standing biomass by fitting three biomass additivity procedures in nine different equations and (2) to compare efficiency in biomass estimates between biomass equations. The analysis was conducted for data on shrubs species collected in 55 quadrats within a 200 km radius of the Tamaulipan thornscrub of Coahuila, Tamaulipas, and Nuevo Leon, in north-eastern Mexico.

2. Materials and methods

The Tamaulipan thornscrub consists of subtropical, semi-arid vegetation that covers parts of the coastal lowlands of north-eastern Mexico. The study was conducted in north-western Coahuila, northern Tamaulipas and eastern Nuevo Leon. The climate of the study area is subtropical in Tamaulipas and eastern Nuevo Leon at the piedmont of the eastern Sierra Madre, and semi-arid in north-eastern Coahuila and northern Tamaulipas and northern Nuevo Leon. The region experiences long warm summers and short cool winters. The area has an average altitude of 120–350 m above sea level. Mean weighted long-term annual temperature and precipitation are 22.3  C and 500 mm, respectively (N  var, 1999). Monthly precipitation is distributed uniformly in the north-western portion of the region and bimodal in the eastern slopes of the Sierra Madre Oriental mountain range. The latter region has the first monthly precipitation peak during late spring–early summer and the second peak in late summer–early fall. Cold fronts generate most of the winter rainfall, accounting for less than 10% of the long-term annual average. Pan evaporation approximates 2000 mm.

Soils of the coastal plains of the northern Gulf of Mexico are dominated by (a) Litosols and Rendzins in the sierra mountain range and hilly mesetas of the south-western portion of the area, (b) Yermosols and Xerosols in the western region, (c) Rendzins in hillslopes of the central plains, and (d) Vertisols in the plains of the eastern part of the region. The primary land uses are: (1) native scrub forests (Tamaulipan thornscrub and its different low forest formations) occupying 65% of the total area and coniferous and broadleaf forests covering 6.37% of the total area, and (2) irrigated and dryland agriculture covering 18% of the region (Aranda et al., 1998). Reservoirs, urban area, grasslands, and secondary native scrub forests are the other land uses in the area.

Vegetation of this region is quite dense and diverse, with more than 22 shrub species occurring in 0.1 ha plots (Romero, 1999; Manzano and N  var, 2000). The most abundant life forms are medium and small shrubs. The under story is

composed of sparse annual and perennial herbs and grasses. [Cotecoca-Sarh \(1973\)](#) and [Reid et al. \(1990\)](#) observed that the dominant shrub species of this ecosystem are *Acacia berlandieri* Benth., *A. farnesiana* (L.) Wild., *A. rigidula* Benth., *Calliandra conferta* Gray, *Celtis pallida* Torr., *Condalia hookeri* M.C. Johnst., *Cordia boissieri* DC., *Diospyros palmeri* Scheele, *Diospyros texana* Scheele, *Ehretia anacua* (Ter  n & Berl.) I.M. Johnst., *Eysenhardtia polystachya* (Ort.) Sarg., *Eysenhardtia texana* Scheele, *Forestiera angustifolia* Torr., *Fraxinus greggii* A. Gray, *Gochnatia hypoleuca* DC., *Helietta parvifolia* (Gray) Benth., *Leucophyllum texanum*, *Malpighia glabra* L., *Mimosa biuncifera*, *Pithecellobium pallens*, *Pithecellobium ebano*, *Prosopis laevigata*, *Prosopis glandulosa*, *Schaefferia cuneifolia*, and *Zanthoxylum fagara*. Several of these species distribute in several places in the American continent (*Prosopis* spp, *Acacia* spp, *Diospyros* spp, *Pithecellobium* spp). Several of these species distribute in other plant ecosystems as well, i.e. the Chihuahuan Desert, The Chaco Province, and several other arid, semi-arid, and subtropical plant communities.

2.1. Data collection

In addition to the 55 quadrats, 60 small trees of the most representative species were selectively harvested to incorporate a wider range in dasometric and biomass characteristics. Quadrats were systematically located from north-eastern Coahuila (6), north-western Tamaulipas (6), south-eastern Nuevo Leon (25), and western Tamaulipas (18). In each quadrat, all standing shrubs were measured for basal diameter (*D*) and top height (*H*). In multi-stemmed shrubs (*A. rigidula*, *P. pallens*, *Bernardia myricaefolia*), each stem was considered as a single shrub and measured in diameter and top height. All shrubs were felled and separated into leaves, branches, and main stem. Stem was considered as the main upright portion of the plant below the first branch with a diameter 1/3 larger than the basal diameter of the stem. Branches were considered all woody portions of the canopy above the stem. Each biomass component was weighted fresh, and approximately 10% of each component randomly selected was taken to the laboratory of the Facultad de Ciencias Forestales of University of Nuevo Leon for oven-dry analysis. Biomass measurement and sampling were done simultaneously for each individual plant within each quadrat.

2.2. Studied shrub species

A total of 30 woody, shrub species were recorded in all quadrats. The 15 species of low frequency with less than 15 individuals were grouped and called the other species group (Other spp). The average and standard deviation of basal diameter, top height, and canopy cover are reported in [Table 1](#). In addition to this information, biomass data collected in the Tamaulipan thornscrub of the area of Linares and reported by [N  var et al. \(2002\)](#) for 10 shrub species were also used in developing the biomass equations with the objective of increasing the sample size and improve the robustness of the equation parameters. Data collected for this study accounted for

Table 1

Characteristics of the shrub species of the Tamaulipan thornscrub of north-eastern Mexico used for fitting the additive biomass equations

Code/species	n	Basal diameter (cm)		Top height (m)		Canopy cover (m ²)	
		Mean	S.D.	Mean	S.D.	Mean	S.D.
1/ <i>A. berlandieri</i>	79	6.74	2.54	4.02	1.41	2.8	2.9
2/ <i>A. farnesiana</i>	18	11.58	11.04	5.01	2.05	1.2	0.9
3/ <i>A. rigidula</i>	78	5.62	3.00	2.93	1.04	1.6	1.4
4/ <i>B. myricaefolia</i>	52	2.39	0.94	1.86	0.39	1.1	0.6
5/ <i>C. pallida</i>	27	5.44	2.11	4.45	1.19	3.6	3.8
6/ <i>C. hookeri</i>	29	7.76	6.64	3.72	1.34	1.2	0.9
7/ <i>C. boissieri</i>	96	9.95	3.60	3.66	0.83	4.6	3.1
8/ <i>D. texana</i>	63	9.18	5.11	3.91	0.94	3.5	3.2
9/ <i>E. polystachya</i>	42	4.74	2.96	3.46	1.63	1.1	1.3
10/ <i>F. angustifolia</i>	18	2.45	1.73	2.24	0.37	1.1	1.2
11/ <i>G. hypoleuca</i>	29	8.18	4.84	3.05	0.84	2.6	2.5
12/ <i>H. parvifolia</i>	72	7.32	3.85	3.86	1.16	2.0	1.6
13/Other species	86	3.99	3.08	2.59	1.68	3.1	4.6
14/ <i>P. ebano</i>	16	14.96	10.32	4.65	1.41	3.2	2.8
15/ <i>P. pallens</i>	123	6.90	3.74	4.47	1.57	3.2	2.8
16/ <i>P. glandulosa</i>	38	10.51	6.36	2.99	1.05	6.0	6.3
17/ <i>Prosopislaevigata</i>	29	14.70	8.27	4.63	1.43	1.3	1.7
18/ <i>Z. fagara</i>	18	5.26	2.03	4.69	1.04	3.3	3.2
Average	51	7.65	4.56	3.68	1.19	2.6	2.5

Other species: *A. madrensis*, *A. texana*, *A. wrightii*, *C. berlandieri*, *C. gallina*, *C. spp*, *K. humboldtiana*, *L. frutescens*, *P. angustifolia*, *Z. obtusifolia*, and 2 other unknown spp.

84% of all the information (762 shrubs) and the rest 26% by data previously reported (151 shrubs) in N  var et al. (2002). Combination of data provided more reliable equation parameters because most species increased the number of shrubs by an average of 30%.

2.3. Procedure

In this research, three additive procedures were used to estimate parameters for the biomass component and total biomass equations: (i) using the same independent variables for estimating each component, (ii) adding the best regression functions of each biomass component, and (iii) seemingly unrelated regression. Seemingly unrelated regression, also called joint-generalized least squares (Cunia and Briggs, 1984, 1985), is a procedure for iteratively forcing the sum of the component coefficients to equal the equation for total biomass. Equation parameters were estimated for each of 17 single species that had data for more than 15 shrubs. For the rest of the species with less than 15 plants a single equation was fitted. A single

additive equation for all species, called the equation for the plant community, was also fitted.

2.4. Equations and methods of parameter estimation

Different methods were used to analyse each procedure. All of three methods focus on estimates using basal diameter (D), top height (H), and the combined variable D^2H as independent variables since a graphical and statistical analysis of the independent variables indicated that D and the combined variable D^2H consistently explained most of the biomass component variation. Therefore, additive procedure (i) was developed in three different equation forms: (1) fitting ordinary nonlinear least-squares procedures using D , ONL, (Eq. (1)); (2) fitting the log-transformed linear least-squares procedures using D^2H , SLog, (Eq. (2)); and (3) fitting the simple linear regression using D^2H , SLin, (Eq. (3)). The best individual biomass component regression equation in additive procedure (ii) was analysed using four approaches to stepwise multiple linear regression: (1) multiple linear stepwise procedure, MSLin, (Eq. (4)), (2) multiple log-transformed stepwise regression procedure, MSLog (Eq. (5)), (3) linear covariance model with dummy variables, CovLin (Eq. (6)), and (4) log-transformed covariance model with dummy variables, CovLog (Eq. (7)). Additive procedure (iii) calculates a set of regression functions such that the total-tree regression is a function of all independent variables used in the individual component regression equations. Parameters of component equations developed in MSLin and MSLog were forced to add the total biomass regression equation and these were called (a) seemingly unrelated linear regression, SurLin, and (b) seemingly unrelated log-transformed regression, SurLog, respectively. MSLin and SurLin, and MSLog and SurLog procedures have the same independent variables but different parameter estimates. Because stepwise regression analysis was conducted in additive procedure (ii), only the variables that statistically explained part of the total biomass variance were included in the equations ($p = 0.15$). The additive equations are defined below in a general format for Eqs. (4)–(7) since biomass components of different species are statistically described by different independent variables. Besides using D , H , D^2H , their log transformations were used as explanatory variables. Covariance analysis, expressed in Eqs. (6) and (7), is a statistical procedure that allows the simultaneous estimation of a set of equation parameters (i.e. for leaf, branch, stem, and total biomass) with the aid of dummy variables. It is an expansion of additive procedure (ii) because with the aid of dummy variables it computes simultaneously parameters of biomass components. Cunia and Briggs (1985) defined a similar procedure as harmonization

$$\begin{aligned}
 \hat{y}_{\text{leaf}} &= b_{10}(D^2H)^{b_{11}}, \\
 \hat{y}_{\text{branch}} &= b_{20}(D^2H)^{b_{21}}, \\
 \hat{y}_{\text{stem}} &= b_{30}(D^2H)^{b_{31}}, \\
 \hat{y}_{\text{total}} &= \hat{y}_{\text{leaf}} + \hat{y}_{\text{branch}} + \hat{y}_{\text{stem}},
 \end{aligned}
 \tag{1}$$

$$\begin{aligned}
\ln \hat{y}_{\text{leaf}} &= \ln b_{10} + b_{11}(\ln D^2 H), \\
\ln \hat{y}_{\text{branch}} &= \ln b_{20} + b_{21}(\ln D^2 H), \\
\ln \hat{y}_{\text{stem}} &= \ln b_{30} + b_{31}(\ln D^2 H), \\
\hat{y}_{\text{total}} &= e^{\ln \hat{y}_{\text{leaf}}} + e^{\ln \hat{y}_{\text{branch}}} + e^{\ln \hat{y}_{\text{stem}}},
\end{aligned} \tag{2}$$

$$\begin{aligned}
\hat{y}_{\text{leaf}} &= b_{10} + b_{11}(D^2 H), \\
\hat{y}_{\text{branch}} &= b_{20} + b_{12}(D^2 H), \\
\hat{y}_{\text{stem}} &= b_{30} + b_{13}(D^2 H), \\
\hat{y}_{\text{total}} &= \hat{y}_{\text{leaf}} + \hat{y}_{\text{branch}} + \hat{y}_{\text{stem}},
\end{aligned} \tag{3}$$

$$\begin{aligned}
\hat{y}_{\text{leaf}} &= b_{10} + b_{11}(D^2 H) + \dots + b_{1k}(H) + b_{12}(\ln D^2 H) + \dots + b_{1n}(\ln H), \\
\hat{y}_{\text{branch}} &= b_{20} + b_{21}(D^2 H) + \dots + b_{2k}(H) + b_{2k+1}(\ln D^2 H) + \dots + b_{2n}(\ln H), \\
\hat{y}_{\text{stem}} &= b_{30} + b_{31}(D^2 H) + \dots + b_{3k}(H) + b_{3k+1}(\ln D^2 H) + \dots + b_{3n}(\ln H), \\
\hat{y}_{\text{total}} &= \hat{y}_{\text{leaf}} + \hat{y}_{\text{branch}} + \hat{y}_{\text{stem}},
\end{aligned} \tag{4}$$

$$\begin{aligned}
\ln \hat{y}_{\text{leaf}} &= b_{10} + b_{11}(D^2 H) + \dots + b_{1k}(H) + b_{12}(\ln D^2 H) + \dots + b_{1n}(\ln H), \\
\ln \hat{y}_{\text{branch}} &= b_{20} + b_{21}(D^2 H) + \dots + b_{2k}(H) + b_{2k+1}(\ln D^2 H) + \dots + b_{2n}(\ln H), \\
\ln \hat{y}_{\text{stem}} &= b_{30} + b_{31}(D^2 H) + \dots + b_{3k}(H) + b_{3k+1}(\ln D^2 H) + \dots + b_{3n}(\ln H), \\
\hat{y}_{\text{total}} &= e^{\ln \hat{y}_{\text{leaf}}} + e^{\ln \hat{y}_{\text{branch}}} + e^{\ln \hat{y}_{\text{stem}}},
\end{aligned} \tag{5}$$

$$\begin{aligned}
\hat{y}_{\text{total}} &= b_0 + b_{11}(D^2 H) + \dots + b_{1k}(H) + b_{12}(\ln D^2 H) + \dots + b_{1n}(\ln H) \\
&\quad + b_{21}(D^2 H) + \dots + b_{2k}(H) + b_{2k+1}(\ln D^2 H) + \dots + b_{2n}(\ln H) \\
&\quad + b_{31}(D^2 H) + \dots + b_{3k}(H) + b_{3k+1}(\ln D^2 H) + \dots + b_{3n}(\ln H),
\end{aligned} \tag{6}$$

$$\begin{aligned}
\ln \hat{y}_{\text{total}} &= b_0 + b_{11}(D^2 H) + \dots + b_{1k}(H) + b_{12}(\ln D^2 H) + \dots + b_{1n}(\ln H) \\
&\quad + b_{21}(D^2 H) + \dots + b_{2k}(H) + b_{2k+1}(\ln D^2 H) + \dots + b_{2n}(\ln H) \\
&\quad + b_{31}(D^2 H) + \dots + b_{3k}(H) + b_{3k+1}(\ln D^2 H) + \dots + b_{3n}(\ln H), \\
\hat{y}_{\text{total}} &= e^{\ln \hat{y}_{\text{total}}},
\end{aligned} \tag{7}$$

where \ln is the natural logarithm.

The total variance for additive equations was conventionally determined by the summation of the squared residuals. Six statistics widely recommended were used for the evaluation of the goodness of fit and for comparisons of alternative biomass models the fit index or coefficient of determination (r^2), the standard error (Sx), the coefficient of variation (CV), the Furnival index (FI), the percent standard error ($S(\%)$), and the percent error (Pe). The goodness-of-fit equations is reported as

follows:

$$r^2 = 1 - (RSS/TSS), \quad RSS = \sum_{i=1}^n (Y_i - \hat{Y}_i)^2, \quad TSS = \sum_{i=1}^n (Y_i - \bar{Y})^2, \\ \bar{Y} = \left[\sum_{i=1}^n y_i \right] / n. \quad (8)$$

$$Sx = \sqrt{RSS/(n-p)}, \quad (9)$$

$$CV = (Sx/\bar{Y}) \times 100, \quad (10)$$

$$FI = [f'(Y)]^{-1} \times \sqrt{\sum_{i=1}^n (Y_i - \hat{Y}_i)^2 / n - p}, \quad (11)$$

$$S(\%) = \frac{100}{n} \sum_{i=1}^n |Y_i - \hat{Y}_i| / \hat{Y}_i, \quad (12)$$

$$Pe = \left[\frac{(196)^2}{\chi^2_{(n-p)}} \sum_{i=1}^n \left\{ \frac{\hat{Y}_i}{\bar{Y}_i} - 1 \right\}^2 \right]^{1/2}, \quad \chi^2_{(v)} = 0.853 + v + 1.645(2v-1)^{1/2}, \quad (13)$$

where n is the number of observations, \hat{Y}_i the estimated total biomass (kg), Y_i the observed total biomass (kg), p the number of coefficients or statistical parameters to be estimated, v the $n - p - 1$ and f' the derivative with respect to biomass and the brackets signify the geometric mean.

These statistics were estimated for total biomass, rather than for each biomass components separately. A disadvantage of estimating the total biomass variance is that users interested in a particular biomass component are not able to assess the goodness of fit of the equations for the components. The variance of total biomass has to be in conventional biomass units (kg tree⁻¹). [Cunia and Briggs \(1985\)](#) and [Parresol \(1999\)](#) suggested a correction factor when using transformations of biomass data. In this report, the correction factor given by $\exp(\sigma^2/2)$ (where σ^2 is the model variance) was used in equations that used log transformations in both dependent and independent variables. Finally, the statistics were estimated with the observed and estimated total biomass in conventional units.

Comparisons between additive equations were conducted to assess the statistical efficiency in estimating total biomass. Statistical efficiency is defined in this report as $((x_i - x_0)/x_0) \times 100$, where x_i is the statistic or biomass of the equation i and x_0 is the statistic of the equation with the best estimator or smallest total biomass variance.

At the quadrat scale, biomass estimates using each of nine additive equations were also contrasted to measured biomass. In addition to the average quadrat biomass (Mg ha⁻¹), the confidence intervals at 95% were also estimated to statistically determine similitude between measured and estimated biomass figures. Quadrat biomass (Mg ha⁻¹) was estimated as the sum of the biomass of the individual shrubs that comprise the quadrat times a correction factor by quadrat size. This simple

procedure determines the accuracy of using equations at the shrub species or at the plant community scale in inventorying biomass.

3. Results

3.1. Ecological parameters of the studied species

Biomass equations were developed for single species typical of the Tamaulipan thornscrub ecosystem. The frequency, dominance, density and relative importance value (RVI) analysis of the 30 shrub species indicated that *C. boissieri* (RVI = 48), *P. pallens* (RVI = 44), *P. glandulosa* (RVI = 30), *A. berlandieri* (RVI = 27), and *D. texana* (RVI = 27) are the most abundant, most frequent, and most dominant shrub species of all 55 quadrats measured. *P. glandulosa* was found only in 12 quadrats located in the semi-arid climates of the northern part of the states of Coahuila and Tamaulipas and this species is widely distributed in the Chihuahuan Desert as well. The other dominant species are more widely distributed and thus more representative of the Tamaulipan thornscrub. Indeed, some of the common dominant species described above are distributed widely in eastern Nuevo Leon and they belong to the most common floristic groups. Some species such as *C. boissieri*, *H. parvifolia*, and *G. hypoleuca* had been previously correlated with a cutting index because of their importance as timber and fuel wood (Reid et al., 1990).

3.2. Measured biomass components

At the quadrat scale, the average and confidence intervals ($p = 95\%$) for leaf, branch, stem, and total above-ground biomass components were 2.5 ± 0.26 , 27.3 ± 2.67 , 14.6 ± 2.07 , and $44.4 \pm 4.40 \text{ Mg ha}^{-1}$, respectively. That is, leaf, branch and stem biomass components accounted for 5.6%, 61.5%, and 32.8% of the total biomass, respectively. At the individual shrub scale, average leaf, branch, stem, and total biomass components averaged 0.6, 6.0, 2.9, and 9.5 kg. At the single species scale, only nine shrub species had ratios of leaf to total biomass larger than 8% (*G. hypoleuca*, *F. angustifolia* and *H. parvifolia*) and only one species had ratios less than 3% (*C. hookeri*). The species *C. pallida*, *D. texana* and *E. polystachya* recorded stem/total biomass ratios larger than 40%. That is, shrubs typical of the Tamaulipan thornscrub of north-eastern Mexico have most biomass in branches as it has been observed for Chilean semi-arid shrubs by Prado et al. (1986).

3.3. Equations for single shrub species

3.3.1. Comparisons between equations

The MSLin, CovLin, and SurLin equations consistently increased the precision in estimating total biomass as seen by the best mean goodness-of-fit statistics ($r^2 = 0.87$, 0.87 , and 0.85 , $S_x = 3.0$, 2.8 , and $3.0 \text{ kg shrub}^{-1}$, $CV = 37\%$, 36% , and 38% , and $FI = 3.0$, 2.8 , and $3.0 \text{ kg shrub}^{-1}$). When considering only the first four

goodness-of-fit statistics (r^2 , S_x , CV , and FI), the MSLin, CovLin, and SurLin increased efficiency in estimating total biomass in comparison to the rest of the equations applied by 61%, 56%, and 56%. The linear equations (SLin, MSLin, CovLin, and SurLin) better fit total biomass data than the log-transformed equations (SLog, MSLog, CovLog, and SurLog) because the former increased efficiency by 44% in comparison to the log-transformed functions in total biomass.

Different additive equations explained better total biomass for different species. However, the SurLin procedure of estimating parameters recorded the highest goodness-of-fit estimates of r^2 , S_x , and CV for most species (*A. farnesiana*, *A. rigidula*, *C. pallida*, *C. boissieri*, *D. texana*, *F. angustifolia*, *G. hypoleuca*, *H. parvifolia*, *P. pallens*, and *P. glandulosa*). The equation developed in CovLin explained better total biomass for the species *A. berlandieri*, *B. myricaefolia*, *E. polystachya*, and *Z. fagara* as seen by the highest r^2 and the smallest S_x and CV values. For the group of Other spp, the equation developed in CovLog provided the best goodness-of-fit estimates (r^2 , S_x , CV , and FI). The equation developed in nonlinear regression, ONL, appeared to provide the best total biomass estimates for *C. hookeri*. The equations developed in SurLin and CovLin consistently provided the best efficiency in estimating total biomass for 59% and 24% of the studied species. The simple linear or the log-transformed regressions commonly used in most allometric studies did not performed as well as the multiple linear, covariance, and seemingly unrelated regressions.

3.3.2. Biomass estimates for all shrubs measured by species

The measured and estimated total biomass for all shrubs measured for each of the 18 species showed that the linear equations (SLin, MSLin, CovLin, and SurLin) predicted the same total mean biomass as the measured ones for all shrub species, with the exception of the SurLin procedure of estimating parameters for *E. polystachya* and *Z. fagara*. The rest of the procedures estimated total biomass, which did not differ, on the average, by more than 26% for any equation developed. In particular, the log-transformed equations (SLog, MSLog, CovLog, and SurLog) biased average total biomass by 14% in contrast to the SLin and ONL equations, which biased average total biomass by 1% and 3%, respectively.

In particular, the ONL, SLog, MSLog, CovLog, and SurLog biased total biomass in *A. farnesiana*, *B. myricaefolia*, Other spp, *B. myricaefolia*, *E. polystachya*, and *E. polystachya* by 10%, 28%, 19%, 13%, 98%, and 49%, respectively. *B. myricaefolia*, *E. polystachya* and Other spp recorded the highest average bias when employing these nine equations to estimate total biomass (11%, 21%, and 10%, respectively).

The average observed, average estimated by using a single equation per each species, and the confidence intervals of total quadrat biomass (Mg ha^{-1}) for each of the nine additive equations indicated that none of the average total biomass estimates statistically deviates from the measured ones. However, equations SLog and MSLog deviated most (13.4% and 11.6%) from the mean total biomass. The rest of the equations did not deviate by more than 4% and the ONL equation approximated most to mean measured biomass for all quadrats. That is, linear and

ordinary nonlinear regression procedures estimate total biomass with the highest statistical efficiency.

3.4. The single biomass equation for the plant community

3.4.1. Comparisons between additive equations using a single equation for the plant community

Equations developed in MSLin, CovLin, and SurLin had the best goodness-of-fit average statistics ($r^2 = 0.81$, $S_x = 4.38 \text{ kg shrub}^{-1}$, $CV = 48.7\%$, $S(\%) = 36.7$, and $Pe = 235$). In contrast, the other equations presented r^2 values less than 0.78, S_x values larger than $4.61 \text{ kg shrub}^{-1}$, CV values larger than 51.2%, and $S(\%)$ values larger than 37.7. However, the log-transformed and the ONL equations presented better Furnival and Pe indices.

3.4.2. Biomass estimates using a single equation for the plant community

Additive equations resulted in different estimates of total biomass at the quadrat scale (Mg ha^{-1}) ($p = 0.05$). The linear (SLin, MSLin, CovLin, and SurLin) and the ONL linear regressions produced similar total biomass estimations, and, henceforth, they are unbiased procedures of parameter estimation. The log-transformed equations (SLog, MSLog, CovLog, and SurLog) deviated by 15%, 13%, 10%, and 0%, respectively.

The nonlinear equation of total biomass estimation for all shrubs for all species is presented in Fig. 1 and it is appropriate for shrubs growing in sufficient biomass to fully stocked quadrats. Stocking as defined in here implies full site occupancy observed by the canopy cover of all shrubs and trees and it is not compared with a

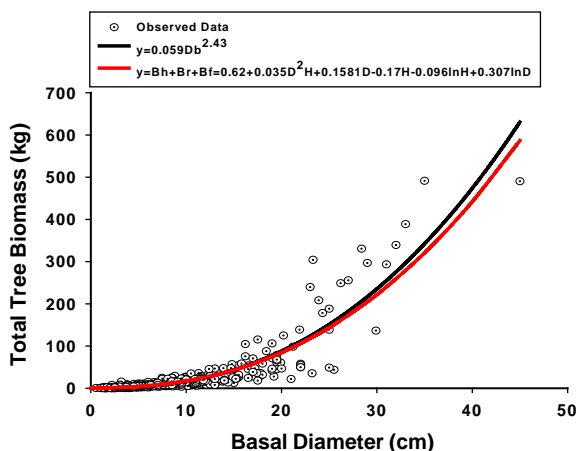


Fig. 1. The relationship between total biomass and basal diameter for 30 species of the Tamaulipan thornscrub of north-eastern Mexico ($n = 913$). Note that the black line represents the conventional nonlinear regression and the red one the seemingly unrelated linear regression equation.

standard of any kind because of the mixture of species and life forms. For shrubs and low trees growing isolated free of competence this equation would likely underestimate total biomass because these trees usually present higher biomass per unit basal diameter as it is seen in several of the upper points for trees with small basal diameter. That is, the slope of this relationship is quite small in comparison to the same relationship developed for other tropical and temperate plant communities (Brown et al., 1989; Schroeder et al., 1997; N  var et al., 2003).

3.4.3. Comparisons between 18 individual equations versus one single equation for the plant community

The overall statistical efficiency was increased by 5% when using 18 different equations even though the average number of parameters increased as an average from 9 in the plant community equation to 110 when using 18 equations. However, when considering the SurLin procedure of estimating parameters and the first three goodness-of-fit statistics (r^2 , Sx , and CV), the efficiency increases when using 18 equations by 12.3% ($r^2 = 7.5$, $Sx = 14.8$, and $CV = 14.7$).

4. Discussion

The SurLin, CovLin, and MSLin allometric equations provided the best goodness-of-fit statistics, increasing statistical efficiency in biomass estimates. For single species with large data samples and large biomass weights, the SurLin procedure increased statistical efficiency on total biomass estimates in contrast to the CovLin procedure. For example, the SurLin procedure had the best goodness of fit for the species (*A. farnesiana*, *A. rigidula*, *C. pallida*, *C. boissieri*, *D. texana*, *F. angustifolia*, *G. hypoleuca*, *H. parvifolia*, *P. ebano*, *P. pallens*, *P. glandulosa*, and *P. laevigata*) that have an average total biomass of 565 kg species⁻¹ and number of observations of 54 observations species⁻¹, respectively. The CovLin procedure improved goodness-of-fit statistics for the remaining species that have an average total biomass of 296 kg species⁻¹ and number of observations of 45 shrubs species⁻¹, respectively. In general, equations developed using SurLin provide reliable total biomass estimates for each of the 18 species used in this report. Regardless of its linearity, when reducing the equations to a single independent variable (D), total biomass was nonlinearly related to basal diameter and was statistically similar ($P = 0.30$) to the line given by the nonlinear conventional allometric model (Fig. 1). Such a nonlinear relationship is commonly observed in similar shrub equations developed elsewhere.

The SurLin procedure meets the characteristics of biomass properties, i.e. total biomass is divided into smaller compartments (bole wood and root) and bole wood is divided into smaller compartments (bark, wood, branch, leaf, etc.). The advantages of using additive equations to estimate biomass components and total biomass include (a) prediction for the components sum to the prediction for the total tree, (b) the coefficients are more consistent with smaller confidence limits, and (c) no single biomass compartment is estimated beyond the total biomass (Cunia and Briggs, 1984; Parresol, 1999). On the other hand, there is an increasing need for estimating

biomass compartments for environmental-related issues, productivity, and economic values. Several models, e.g. the CO₂ fix (Mohren and Klein Goldewijkt, 1990) require estimates of the relative biomass proportions of leaves, branches, and stems. Land managers require precise and consistent estimates of fuel wood, given by branch and stem biomass, and the carrying capacity for grazing, given by palatable leaf biomass. Foresters require precise estimates of branch and stem biomass for fuel wood estimation, pulp production, and productivity studies (Agee, 1983). By using the total biomass equation for the required compartment, the specific biomass component is directly estimated, i.e. when using the single equation for the plant community $BT = [0.026884 + 0.001191D^2H + 0.044529D - 0.01516H] + [1.025041 + 0.023663D^2H - 0.17071H - 0.09615 \ln H] + [-0.43154 + 0.011037D^2H + 0.113602D + 0.307809 \ln D]$ and the objective is to estimate leaf, branch or stem biomass, then the equation used is described in the first $[0.026884 + 0.001191D^2H + 0.044529D - 0.01516H]$, second $[1.025041 + 0.023663D^2H - 0.17071H - 0.09615 \ln H]$, and third bracket $[-0.43154 + 0.011037D^2H + 0.113602D + 0.307809 \ln D]$, respectively. Independent variables that feed these equations are only basal diameter (D) in cm and top height (H) in m. The results are given in kilograms per shrub or tree. An example of a shrub measuring 30 cm in basal diameter and 6 m in top height will result in 7.70, 127.61, 63.62 and 198.94 kg for leaf, branch, stem, and total biomass, respectively.

Biomass equations provided in Table 2 can be applied to species with the shrub characteristics reported in Table 1. Several equations predict well biomass components in all the range of shrub attributes measured for the species *A. berlandieri*, *C. pallida*, *C. hookeri*, *H. parvifolia*, and Other spp. However, for the remaining species, equations compute adequate biomass figures for shrubs with basal diameter larger than 4 cm and top height larger than 3 m. The equation for all species for all quadrats reported at the end of Table 2 computes well individual shrub biomass figures in all range of measured attributes. Using the single equation for all species typical of the Tamaulipan thornscrub of north-eastern Mexico, leaf, branch, and stem biomass compose approximately 5%, 60%, and 35% of the total shrub biomass. Leaf to total biomass and stem to total biomass ratios slightly decrease with increasing shrub size unlike branch biomass.

Non-additive equations have been developed to estimate total biomass (Brown et al., 1989; Deans et al., 1996) and they do not explore the advantages of the system of linear regressions. Non-additive equations include the use of nonlinear, log-transformed, and polynomial equations (Brown et al., 1989; Deans et al., 1996; Ter-Mikaelian and Korzukhin, 1997), where diameter at breast height is the common independent variable. For our shrubs of the Tamaulipan thornscrub the ONL equation resulted in unbiased total biomass estimates, but it had intermediate goodness-of-fit statistics. Other equations include the variable diameter at breast height, DBH , and top height, H , the combined variable, DBH^2H , wood density and Holdridge life zone as the explanatory parameters (Brown et al., 1989). Diameter at crown base and sapwood area measured at various heights in the stem as independent variables are better predictors of leaf biomass (Clark III, 1982, pp. 119–139; Robichaud and Methven, 1992), and these variables must be further explored using the system of biomass equations.

Table 2

The seemingly unrelated linear regression equations developed in additive procedure (iii) for each of eighteen species and for all species from 55 quadrats in the Tamaulipan thornscrub of north-eastern Mexico

Species	Goodness-of-fit statistics						Seemingly unrelated regression equation
	r^2	Sx	CV	FI	$S(\%)$	Pe	
<i>A. berlandieri</i>	0.76	2.9	31.0	2.9	24	78	$BT = [0.006009 + 0.241108H + 0.000847D^2H - 0.47883(\ln H)] + [1.946 + 0.01667(D^2H)] + [-0.8765 + 0.541821D]$
<i>A. farnesiana</i>	0.95	2.7	23.8	2.7	188	118	$BT = [1.1856 + 0.7046D - 2.9935 \ln D] + [18.48 + 13.01D - 53.9 \ln D] + [-4.4576 + 1.4946D]$
<i>A. rigidula</i>	0.92	1.4	22.2	1.4	22	123	$BT = [0.2984 - 0.3663H + 0.8857 \ln H + 0.001589D^2H] + [1.7299 - 1.7568H + 0.02176D^2H + 1.1115 \ln D^2H] + [0.5772 + 0.011244D^2H]$
<i>B. myricaefolia</i>	0.81	0.5	49.7	0.5	41	133	$BT = [0.1498 - 0.0609D + 0.004448D^2H] + [-3.72131 + 0.248698D + 5.1932H - 10.4555 \ln H] + [-3.72131 + 0.248698D + 5.1932H - 10.4555 \ln H]$
<i>C. pallida</i>	0.95	1.0	16.2	1.0	19	94	$BT = [-0.02387 + 0.071082D] + [0.822031 - 0.3336D + 0.027934D^2H] + [-0.97513 + 0.622086D]$
<i>C. hookeri</i>	0.88	3.2	40.0	3.2	38	138	$BT = [-0.49169 + 0.119894D] + [1.34514 - 0.57648D + 0.036956D^2H - 0.07861 \ln D^2H] + [-2.28529 + 6.281245H + 0.004902D^2H - 14.8795 \ln H]$
<i>C. boissieri</i>	0.70	4.9	36.8	4.9	28	277	$BT = [-0.80889 + 0.708933H + 3.4441 \ln D - 1.52967 \ln D^2H] + [-5.1898 + 4.051755H + 0.953933 - 8.3199 \ln H] + [0.402273 - 0.79265H + 0.429856D + 0.007672D^2H]$
<i>D. texana</i>	0.89	5.2	32.0	5.2	30	82	$BT = [-0.4384 + 0.12124 \ln D^2H + 0.072176H] + [3.32259 + 0.010964D^2H] + [0.937974 + 0.0126D^2H]$
<i>E. polystachia</i>	0.74	2.8	66.9	2.8	1097	228	$BT = [-0.00842 - 0.02042H + 0.06316 \ln D^2H] + [0.912571 - 0.10608H + 0.009052 \ln H + 0.009085D^2H] + [0.089769 + 0.171654H + 0.007258D^2H]$
<i>F. angustifolia</i>	0.98	0.6	26.5	0.6	38	162	$BT = [0.062164 + 0.011566D^2H - 0.05652 \ln D^2H] + [-0.088 + 0.115089D^2H] + [-0.08742 + 0.014452D^2H]$

<i>G. hypoleuca</i>	0.93	3.7	32.5	3.7	17	524	$BT = [-0.69334 + 0.335057 \ln D^2 H] + [-2.18807 + 1.046488 \ln D^2 H + 0.008012 D^2 H] + [-0.10528 + 1.061613 D - 2.68152 \ln D]$
<i>H. parvifolia</i>	0.82	3.0	36.6	3.0	29	224	$BT = [-0.17395 + 0.002432 D^2 H - 1.24942 H + 4.2865 \ln H - 0.18844 \ln D] + [20.99959 + 0.056192 D^2 H - 4.382 H - 1.90569 D] + [3.7336 + 0.025468 D^2 H - 0.094648 D]$
<i>Other species</i>	0.65	7.2	90.9	7.2	5	340	$BT = [-0.05266 + 0.000052 H + 0.092582 \ln D^2 H] + [0.109003 + 0.014021 D^2 H - 1.62531 H + 0.89543 \ln D^2 H] + [0.3558 + 0.010336 D^2 H - 0.51147 D + 1.5063 \ln D]$
<i>P. ebano</i>	0.79	3.1	37.5	3.1	14	103	$BT = [-0.9523 + 0.002317 D^2 H] + [-1.28375 + 0.027484 D^2 H] + [-3.08371 + 0.025196 D^2 H]$
<i>P. pallens</i>	0.79	3.1	37.5	3.1	14	103	$BT = [-0.00523 + 0.000689 D^2 H + 0.8018 \ln D] + [0.332213 + 0.017196 D^2 H - 0.94861 D + 3.388551 \ln D] + [-0.58367 + 0.004255 D^2 H + 0.393071 D]$
<i>P. glandulosa</i>	0.97	3.3	18.0	3.3	31	199	$BT = [-0.15545 + 0.110531 D + 0.000797 D^2 H] + [4.2362 + 3.2482 D - 11.6949 \ln D] + [-2.04254 + 0.387649 D + 0.5166 H]$
<i>P. laevigata</i>	0.87	1.6	46.2	1.6	27	82	$BT = [-0.14775 + 0.000659 D^2 H + 0.118172 D] + [-2.981 + 0.006699 D^2 H + 1.221108 D] + [-0.62634 + 0.001711 D^2 H + 0.313902 D]$
<i>Z. fagara</i>	0.92	3.1	31.4	3.1	33	50	$BT = [0.58283 + 0.000668 D^2 H - 0.29147 \ln H] + [-3.288 + 1.1233 D + 0.84592 \ln H] + [1.08316 + 0.005911 D^2 H - 0.11339 H]$
All species tested ($n = 913$)	0.80	4.4	48.6	4.4	36.7	229	$BT = [0.026884 + 0.001191 D^2 H + 0.044529 D - 0.01516 H] + [1.025041 + 0.023663 D^2 H - 0.17071 H - 0.09615 \ln H] + [-0.43154 + 0.011037 D^2 H + 0.113602 D + 0.307809 \ln D]$

Note: The first, second, and third inner set of brackets estimates leaf, branch and stem biomass components, respectively. Therefore, the sum of these components equals total biomass (BT). Hence, in most cases the equation for total biomass equation could be reduced. \ln = natural logarithm.

Average goodness-of-fit estimates changed between equations at different scales. When adding more species into the equations (i.e. one equation for the plant community), the goodness-of-fit statistics reduces statistical efficiency in estimating total biomass because the total biomass variance increased. Although the number of total estimated parameters was reduced by increasing the number of shrub species into the equations, this mathematical artifact (reducing the model degrees of freedom) did not compensate for the increment of the total biomass variance. Therefore, biomass inventory in the Tamaulipan thornscrub of north-eastern Mexico that requires increased precision must use single equations for each species (Table 2). When coarse approximations are required on biomass components or total biomass a single equation (bottom of Table 2) will increase the coefficient of variation on the average by 12.3% as a result of using the SurLin equation.

5. Conclusions

Equations to estimate above-ground, standing biomass were developed for the plant community and for 18 single species typical of the Tamaulipan thornscrub of north-eastern Mexico. Equations developed using additive procedures in seemingly unrelated linear regression provided better statistical efficiency in total biomass estimates at the individual species and at the plant community scales. Therefore, they are recommended to estimate biomass components and total biomass for the species described. These equations can also be used in forest biomass inventories because they compute similar biomass estimates than the measured ones for 55 quadrats covering a wide range of field conditions within the Tamaulipan thornscrub of north-eastern Mexico, as well as in other arid, semi-arid, and subtropical plant communities with plant species similar to those observed in this plant community.

Acknowledgements

The Mexican Foundation for Science and Technology, CONACyT, and University Fund for Science and Technology, PAICyT, funded this project through research grants 28536-B and CN 323-00, respectively. Dr. Stan Wullschleger and Dr. Rich Norby of the Oak Ridge National Laboratory, Environmental Sciences Division are thanked by their helpful suggestions to improve the manuscript. This report was written during a sabbatical leave of the senior author at the Environmental Sciences Division of the Oak Ridge National Laboratory. Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the US Department of Energy under contract DE-AC05-00OR22725.

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